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THE EFFECT OF DIFFERENT MANAGEMENT PRACTICES ON A GRASSLAND COMMUNITY AND THE RESULTING FATE OF SEEDLINGS

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SUMMARY

The effects of the management practices of hay-making from unmanured grassland in July, in September and in July + September, and of abandoning of formerly manured, hayed and grazed grassland were studied from 1973 onwards. The cover of dominant species strongly fluctuated with «abandoning» and with «July hay-making» as compared to the other regimes. Cover of *Holcus lanatus* on the one hand and of *Ranunculus repens*, *Agrostis stolonifera* and *Poa trivialis* on the other fluctuated complementary. Seedlings emerged in spring with all management practices. Depending on the time of hay-making in late summer and in autumn new seedlings emerged. Most seedlings emerged with «September hay-making» and with «July + September hay-making». Survival was generally related to the dates of emergence and hence to the structure of the vegetation. The trend reveals of relatively much dicots reaching the juvenile stage with «September hay-making», whereas relatively much monocots reach this stage with «July hay-making». Of species sown in November a few individuals reached the flowering stage with «September hay-making» and with «July + September hay-making» regimes.

1. INTRODUCTION

Germination and seedling establishment in grassland came into attention since insight in turnover and dynamic equilibria had been enlarged by detailed analysis of grasslands. Especially the concepts of the "safe site" (HARPER et al. 1961) and the "regeneration niche" (GRUBB 1977) contributed to hypotheses about species density in homogeneous grasslands. "Gaps" i.e. open areas can be filled up either by vegetative spread or by generative reproduction from the seed bank; the latter will be discussed here.

Seeds can disappear by migration, predation, decay, or by germination from a safe site (HARPER 1977). the germinating species can be (i) already present in the plot, (ii) at present nearby in the surrounding vegetation, (iii) disseminated into the community from some distance, or (iv) resulting from the seed bank of lost species. Most seeds are dispersed over a small distance only (LEVIN & KERSTER 1974, TER BORG 1979) and most seedlings in an undisturbed vegetation will originate from the local seed rain. In undisturbed communities with a closed canopy very low seedling densities are found (TAMM 1956, RABOTNOV 1969, MILES 1979, COOK 1979, GRIME 1979). However, gaps may provide safe sites for seedlings in an overall undisturbed community (MILES 1979). Small gaps

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can be created by plants dying, by soil being bared by animal hooves or burrowing animals, larger gaps arise from moles or tractor tracks.

Gap size appeared to be important in generative reproduction. Early establishment of seedlings is greater, but survival after two years is smaller in small patches of bared ground in a heathland vegetation as compared to larger patches, due to quickly overgrowing of small patches (MILES 1974). In grassland vegetation in 25 cm diameter gaps germination is greater than in smaller gaps, at least partly due to the increased diurnal fluctuations of superficial soil temperature (Thompson in GRIME 1979, THOMPSON, GRIME & MASON 1977), partly to the influence of light. The micro-environment within a closed turf is indeed different from that of an open turf or a gap. In the turf the higher humidities could favour pathogenic attack of seeds and seedlings, and could provide a more suitable environment for potential predators (SAGAR & MORTIMER 1976).

A dense turf sometimes hinders seedling emergence and always survivorship of *Juncus effusus* (LAZENBY 1955), *Plantago* spp. (SAGAR & HARPER 1960, BLOM 1977), *Rumex* spp. (CAVERS & HARPER 1967), *Bellis perennis* (HARPER 1977), *Taraxacum* sp. (MØLGAARD 1977) and *Trifolium repens* (HARPER 1977, TURKINGTON et al. 1979). Fluctuations in the density of the turf throughout the year create changing conditions for germination of seeds and establishment of seedlings. Thus the character of safe sites for germination and seedlin establishment could depend on the structure of the vegetation and its small scale disturbances. This is affected by management practices such as mowing regimes. Management practices can also affect the overall species composition of the vegetation (HARPER 1971).

This study describes the fate of seedlings in grasslands under different management practices and is part of a study into the changes in composition of the vegetation of grasslands caused by different management practices and the influence of composition of seed bank, germination and seedling establishment.

2. MATERIALS AND METHODS

The study area, a grassland lot (0.5 ha) in the nature reserve "Stroomdallandschap Drentsche A" (53°05′ NL, 6°40′ EL) in the Netherlands, was acquired by the State in 1972 (BAKKER 1976a). In the beginning of this century it was reclaimed from wet heathland and it gradually became more productive. Haymaking and grazing were practised for several decades.

The study area has a sandy soil with a ground water level between – 20 cm in winter and – 100 cm in summer (cf. BAKKER 1976b, GROOTJANS 1980). Manuring ceased in 1973 and various experimental managements were imposed viz. haymaking in July, in September in July + September and abandoning.

From 1975 onwards the above ground standing crop and litter has been determined just before hay-making by clipping ten randomly chosen plots (20 × 20 cm) at each management site (10 × 50 m).

Annual changes in the vegetation were recorded (LONDO 1976) in two permanent plots (2 × 2 m) at each management site in June, from 1973 onwards. In

order to registrate seasonal fluctuations of the vegetation a third permanent plot was recorded every six to eight weeks from September 1975 onwards. Close to this permanent plot and in addition to this registration, seedlings were marked individually and recorded at five replicate permanent plots (10 × 10 cm) from March 1977 onwards. Seedling is defined as the stage with cotyledons and first (pair of) leave(s). This approach remains only tentative since seedlings may have emerged and disappeared in the six week interval between two recordings. Some measure of the bias of overlooking seedlings was gained by five close investigations (LINKOLA 1930) in the period of March 1977 to April 1978 of five replicate field-taken sods (10 × 10 cm each).

To investigate the influence of different mangement practices upon the germination and establishment of species new to the vegetation (as far as could be judged) and in the seed bank (which had been determined in another experiment) 30 species were sown in November 1977. The seeds had been collected in the same year and were kept dry at 4 °C. Each of three replicate plots of 10 × 10 cm at each management site was seeded with 100 seeds of each species. Every four weeks the numbers of seedlings were recorded. In June 1978 all introduced species seedlings and juveniles were removed.

Nomenclature of species follows HEUKELS & VAN OOSTSTROOM (1975).

3. RESULTS

3.1. Changes in cover, species diversity and standing crop

The vegetation of the study area in 1973 mainly consisted of *Agrostis spp.*, *Poa pratensis*, *Holcus lanatus*, *Poa trivialis*, *Festuca pratensis*, *Ranunculus repens*, *Festuca rubra*, *Lolium perenne*, *Taraxacum sp.*, *Cardamine pratensis*, *Cerastium holosteoides*, *Alopecurus geniculatus* and *Rumex acetosa* in order of decreasing abundancy. It has representatives of the vegetation of moist, well-manured pastures (*Arrhenatheretalia*) and of disturbed environments (*Agropyro-Rumicion crispi* (WESTHOFF & DEN HELD 1969, ARNOLDS & VAN DER MEIJDEN 1976).

Changes in mean cover of the principal species in two permanent plots since 1973 at each management site are shown in *fig. 1*. The increase of *Holcus lanatus* in the first two years as well as its decrease in 1979 constitutes a general phenomenon. Except for the first years «September hay-making» and «July + September hay-making» result in the co-dominance of several species, whereas «abandoning» and «July hay-making» keep *Holcus lanatus* dominating.

Changes in the cover of the principal species in the permanent plots recorded every six weeks from 1975 onwards are shown in *fig. 2*. Annual fluctuations of the dominant species are especially high with «abandoning» and with «July hay-making» caused by the dominance of *Holcus lanatus* during the summer period and litter accumulation in winter. *Ranunculus repens*, *Poa trivialis*, *Agrostis* spp., *Cirsium arvense*, *Cardamine pratensis* and *Rumex acetosa* show complementary fluctuations.

The number of species at the beginning of the experiments was about 12 (*fig.*

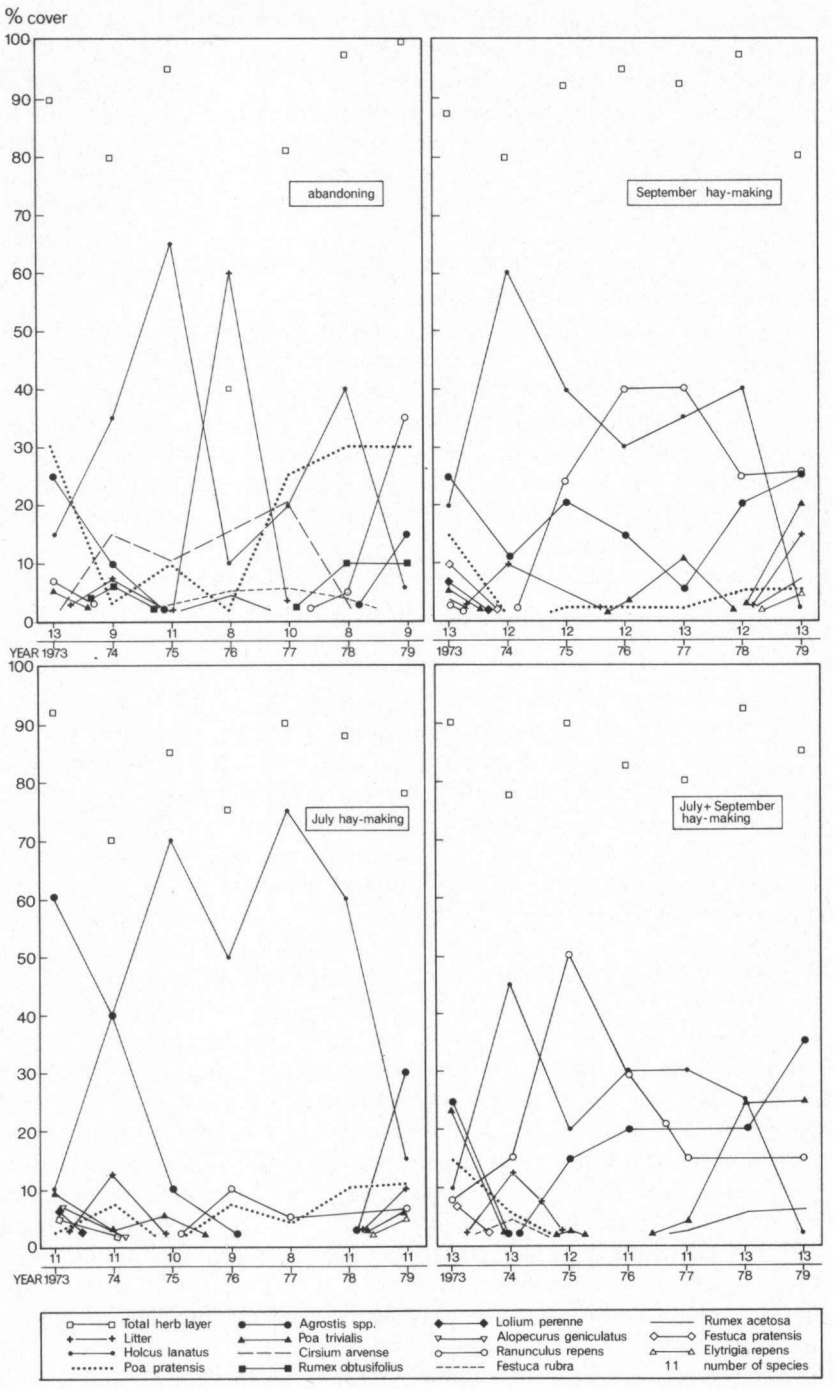

Fig. 1. Cover % of principal species at different management practices from 1973–1979 (1973 recorded mid-May, other years June).

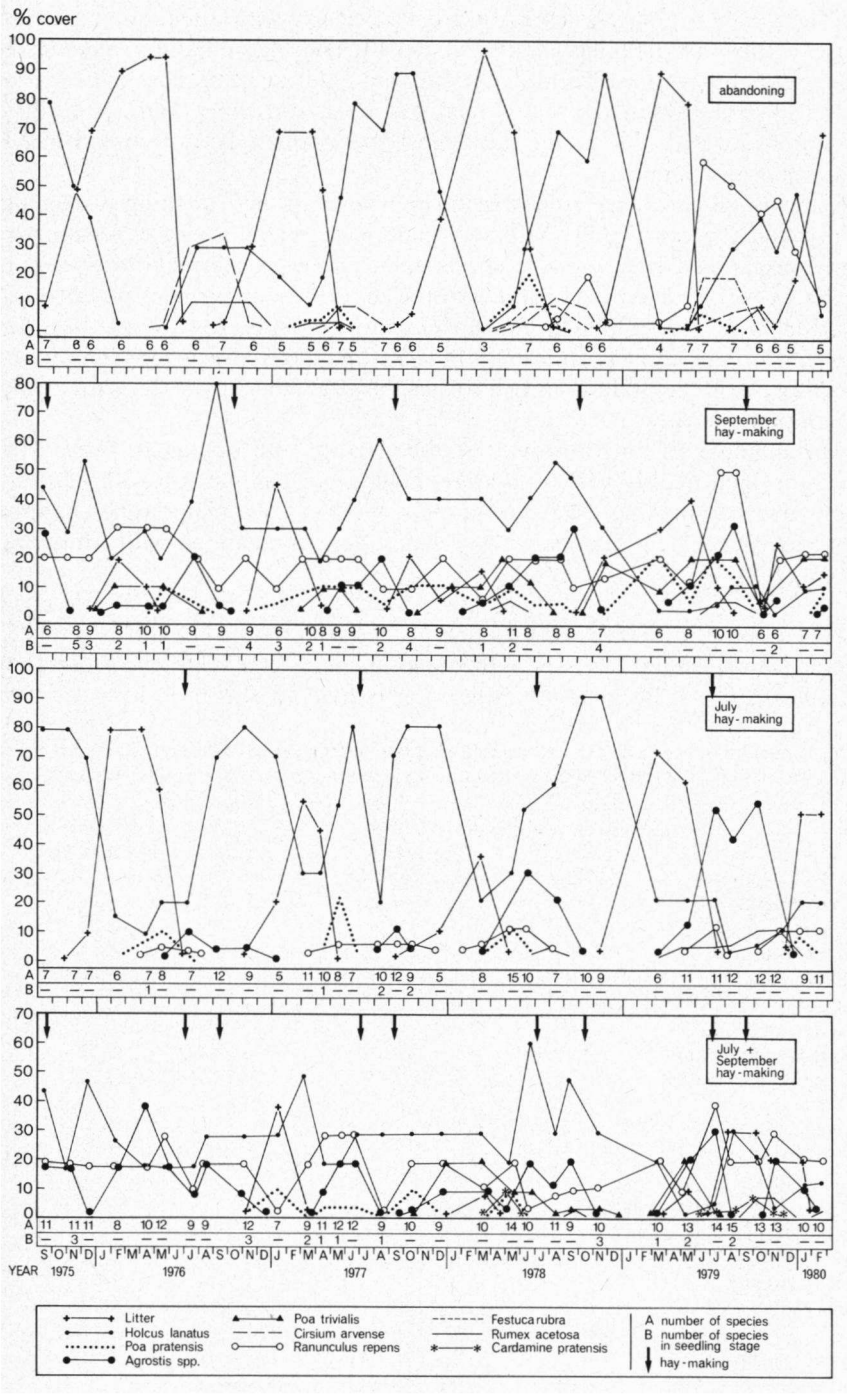

Fig. 2. Cover % of principal species at different management practices from 1975–1979. Numbers along the X-axis indicate the total number of species present, and the number of which seedlings are also present.

1). The number of species tends to decrease clearly with «abandoning», fluctuates with «September hay-making» and with «July hay-making», but tends to increase slightly with «July + September hay-making«. Most species have been found in spring when the turf is relatively open and short. With «July hay-making», however, in several years most species have been recorded in late summer or in autumn.

Some trends can be recognized in the number of species emerging as seedlings in permanent plots (*fig. 2*). With nearly all management practices seedlings of some species have been found in spring and again after hay-making. Species of which seedlings have been found with the different management practices are listed in *table 1*. Seedlings of *Holcus lanatus*, *Poa* spp., *Rumex acetosa*, *Cardamine pratensis* and *Cerastium holosteoides* are quantitatively most important. Most species in the seedling stage have been found with «July + September hay-making» in the course of years.

The quantity of above ground standing crop, litter included, (*table 2*) is generally high in July with «July hay-making» in comparison with «July + September hay-making». Except for 1978, most organic material has been removed with «July + September hay-making» in comparison with «July hay-making».

3.2. Seedling density and survival

Changes in seedling densities with different management practices are summarized in *fig. 3*. Because the number of individual species is low, the total

Table 1. Seedlings recorded in several permament plots (see text) at different management practices during the period 1973–1980.* Species absent in the vegetation before registration as a seedling.

	abandoning	September hay-making	July hay-making	July + September hay-making
Holcus lanatus	+	+	+	+
Poa spp.	+	+	+	+
Rumex acetosa	+	+	+	+
Ranunculus repens	+	+	+	+
Cardamine pratensis	+	+	+	+
Festuca rubra	+			+
Epilobium tetragonum*	+			
Cerastium holosteoides		+	+	+
Agrostis spp.		+	+	
Rumex obtusifolius			+	
Stellaria media*			+	+
Taraxacum sp.			+	+
Anthriscus sylvestris			+	+
Festuca pratensis				+
Juncus bufonius*				+
Stellaria alsine*				+
Lotus uliginosus*				+
Number of species	7	7	11	14

Table 2. Mean above ground standing crop before hay-making (gdw.m^{-2}) of ten randomly chosen plots of 20 × 20 cm each. Standard deviation in parentheses.

	July hay-making	September hay-making	July + September hay-making
1974	580 (50)	?	605 (55) + ?
1975	820 (105)	700 (70)	810 (100) + 340 (30)
1976	725 (210)	655 (290)	600 (160) + 250 (70)
1977	775 (140)	?	655 (145) + ?
1978	940 (220)	600 (150)	810 (175) + 225 (40)
1979	340 (120)	490 (205	295 (85) + 180 (65)

numbers of seedlings are taken. Generally large numbers of seedlings are found in spring and also after hay-making large numbers of new seedlings may emerge. Most monocots emerge in autumn, most dicots after hay-making except for «abandoning», where they tend to emerge in spring. All species appear throughout the year. The total number of seedlings sampled from field-taken sods is larger than that from field plots; the ratio monocots: dicots is also larger in the field-taken sods. The list of species concerned is identical.

Survivorship curves of cohorts of seedlings of all species with different management practices are given in *fig. 4*. Seedlings reaching the juvenile stage (second (pair of) leave(s)) have been registered separately; their fate was not recorded. The total number of seedlings and juveniles has been summarized in *table 3*. Management practices differ not significantly, but some trends can be discerned (i) most seedlings emerge with «September hay-making» and with «July + September hay-making», (ii) most seedlings reach the juvenile stage with «September hay-making» and with «July hay-making», with high percentages for dicots and monocots, respectively, (iii) seedlings emerging after hay-making often pass into the juvenile stage, (iv) early-spring seedlings more often reach juvenile stages than those from late-spring cohorts, (v) some autumn seedlings can persist during the whole winter half of the year.

Thirty species not found in the vegetation or in the seed bank, have been

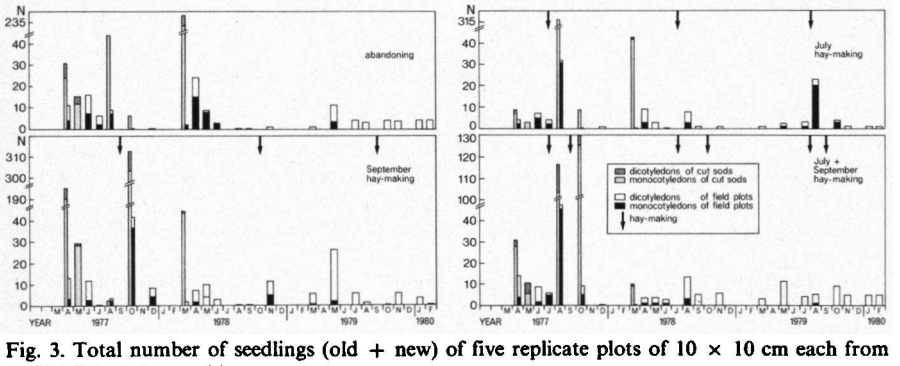

Fig. 3. Total number of seedlings (old + new) of five replicate plots of 10 × 10 cm each from 1977–1980. ↓ hay-making.

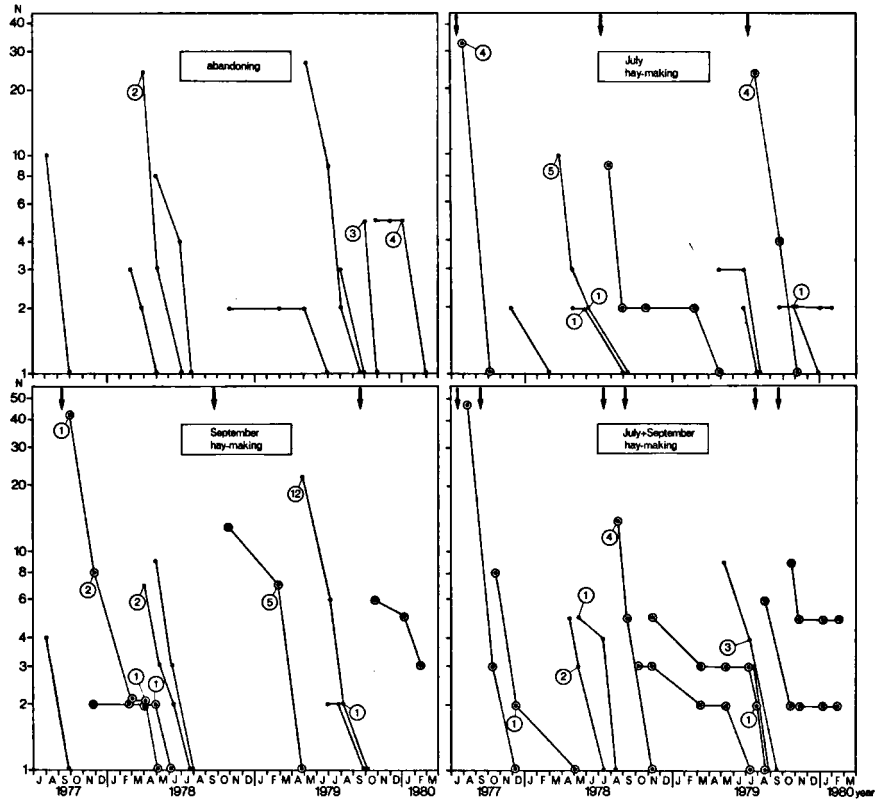

Fig. 4. Survivorship curves, log (N + 1), of cohorts of seedlings (all species taken together) at different management practices of five replicate plots of 10 × 10 cm each.
④juveniles, ↓ hay-making, encircled points indicate cohorts emerged after hay-making.

Table 3. Mean number of seedlings and juveniles of five replicate plots of 10 × 10 cm each at different management practices during the period August 1977 to February 1980.
T: total, M: monocots, D: dicots
Standard deviation in parentheses.

	number of seedlings			number of juveniles			percentage of juveniles		
	T	M	D	T	M	D	T	M	D
abandoning	15.6(12.5)	6.4(5.9)	9.2(13.0)	1.8(2.9)	0.2(0.4)	1.6(3.0)	11.2(20.1)	1.2(2.7)	13.4(28.3)
September hay-making	19.6(5.3)	10.0(4.8)	9.6(3.5)	5.0(3.6)	0.6(0.9)	4.4(3.9)	29.2(28.2)	4.8(7.5)	45.4(30.2)
July hay-making	15.6(6.6)	12.2(7.2)	3.4(1.1)	3.2(4.6)	2.6(3.9)	0.6(0.9)	20.2(25.0)	16.8(25.0)	24.0(43.3)
July + September hay-making	21.0(6.6)	11.0(4.3)	10.0(6.2)	2.4(0.9)	0.8(1.3)	1.6(1.3)	11.2(3.3)	5.4(7.8)	17.8(12.1)

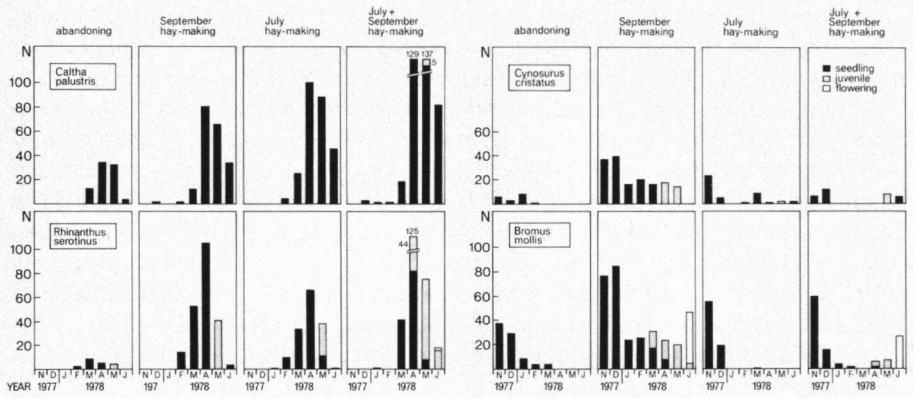

Fig. 5. Total number of seedlings (old + new) of three replicate plots of 10 × 10 cm each with 100 sown seeds in November 1977.

introduced by sowing. The results, exemplified by four species, are shown in *fig. 5*. It appears that the dicots germinate from february onwards, while the monocots germinate in autumn as well as in spring. With «September hay-making» and with «July + September hay-making» seedling emergence was quick and in large quantities, whereas some seedlings became juvenile and even reached the flowering stage.

4. DISCUSSION

4.1 Changes in cover, species diversity and standing crop

The former agricultural practices implied manuring, hay-making with several cuts, the first at the end of May, and grazing in late summer. These practices effectively prevent *Holcus lanatus* becoming a dominant species (Riveros in WATT 1978). All experimental management practices are abrupt changes from this former agricultural practices, leading towards an explosive increase of *Holcus lanatus* (cf. BAKKER 1976b), a phenomenon also described by VAN DEN BERGH (1979). This change may have been caused by hay-making after the dispersal of seeds of *Holcus lanatus* (OOMES 1976, 1977), or by rapid vegetative spread smothering out competitors (WATT 1978). Demographic data are lacking as yet. The yearly fluctuations of the dominant species can tentatively be arranged according to increasing amplitudes as «July + September hay-making», «September hay-making», «July hay-making» and «abandoning». An identical series could be made with regard to increasing deviation from the former agricultural practices. This affirms the hypothesis that the larger the change in management practice (or, more generally, environmental circumstances), the larger the changes in the vegetation and the decrease in the number of species will be (VAN LEEUWEN 1966, WESTHOFF 1971, BAKKER 1979, RIJKSINSTITUUT VOOR NATUURBEHEER 1979, WESTHOFF & SYKORA 1979).

The sudden decline of *Holcus lanatus* in 1979 (*fig. 1*) could be caused by the

preceding severe winter and wet spring. De Vries & 'T Hart (in WATT 1978) found that after severe frost *Holcus lanatus* was killed and replaced by *Phleum pratense* and *Poa trivialis*. The wet spring could have lowered the N-mineralization-rate resulting in a low NO_3^--content and a low *Holcus lanatus* cover. It has been demonstrated elsewhere that the reverse process, i.e. lowering of the ground water table, increases the N-mineralization-rate and the NO_3^--content, accompanied by a strong dominance of *Holcus lanatus* (GROOTJANS 1979a, b). The complementary fluctuations of *Holcus lanatus* on the one hand and of *Ranunculus repens* and *Agrostis stolonifera* on the other (*figs. 1* and *2*) fit in RABOTNOV's (1975) system of "violents" (competitors sensu GRIME 1979) (*Holcus lanatus*) and "explerents" (ruderals sensu GRIME 1979) (*Ranunculus repens* and *Agrostis stolonifera* with above ground runners) in which luxurious growth of explerents is connected with a decrease in violents.

In the experimental period the above ground standing crop before haymaking (*table 2*), litter included, generally remains high. Lower standing crop with «September hay-making» as compared to the other management practices may be attributed to leaf senescence and decomposition; in a dense grassland community dead leaves may seriously depress growth rates (LANGER 1972, GRIME 1979). Most removal of organic material occurs with «July + September hay-making» (the amounts of nutrients removed are not known); lowering of the hay production apparently needs time. On sandy and clayey soils and with comparable management practices OOMES (1976, 1977) found after several years a considerable reduction of standing crop from 1000 to 500 gdw.m^{-2}, but no increase in the number of species. In this study a slight increase in the number of species could be observed with «July + September hay-making» at a standing crop well over 500 gdw.m^{-2}, which is considered high (KLAPP 1965).

4.2. Seedling density and survival

The number of seedlings found in field-taken sods (*fig. 3*) generally exceeds the densities found in the field. LINKOLA (1930) reporting a comparable study in grassland communities, reaches the same conclusion. Monocots appear to be overlooked to a large extent in field plots, but even then considerable amounts of seedlings have been found throughout the year. Seedlings numbers reach a peak in spring and autumn (*figs. 3* and *4*), representing the spring germinators and autumn germinators described by GRIME (1979). GRIME mentions an immediate germination of all seeds of the autumn germinators, but part of them germinates in spring pointing to polymorphism with respect to germination requirements (GRIME 1979), or various safe sites. Seedling emergence of sown species (*fig. 5*) shows the same phenomenon, but also demonstrates its dependence on management practices, since only with «September hay-making» and with «July haymaking» new seedlings emerge in spring.

Two categories of seedlings are found (*table 1*): (i) seedlings of species already present in the vegetation and (ii) seedlings of species absent in the vegetation. Seedlings of the first category may contribute to the turnover of present species via the regeneration niche (GRUBB 1977), whereas seedlings of the second ca-

tegory may contribute to the establishment of new species. These seedlings either come from outside the study area, by anemochorous, zoochorous or anthropochorous dispersal, or from the seed bank. Some species that might be expected in the studied grassland communities, but are lacking as yet, depend on introduction from outside the study area as is demonstrated by the sowing experiments.

Little is known about the causes of seedling mortality. A general notion suggests that in grassland with a dense canopy seedling survival is negligible. In most cases, moss and litter adversily affect seedlings (RABOTNOV 1969). They may suffer pathogenic attack and/or predation (SAGAR & MORTIMER 1976), especially by invertebrates (Mortimer in WATT 1978). Seedlings emerging on deep litter are more prone to microbial attack (GRIME 1979) and often are killed by desiccation before roots reach the soil (GRUBB 1977). COOK (1979) mentions grazing herbivores, pathogens and drought stress as important mortality factors. The supposed inhibition of the growth by decomposing roots especially after hay-making (*Rumex acetosa*, NEWBERY 1979) and/or litter needs research.

The phenomenon of seedlings remaining in the seedling stage for several months (persistent slow-growing seedlings sensu GRIME (1979) has been reported as well for woodland species (TAMM 1956).

4.3 Vegetation dynamics and the fate of seedlings

The dominating *Holcus lanatus* probably is responsible for the large standing crop, because of the decline of standing crop and corresponding low cover of *Holcus lanatus* in the extreme year 1979. It might be expected that *Holcus lanatus* will dominate anew under mean climatological circumstantes (RABOTNOV 1975) at the cost of *Ranunculus repens* and *Agrostis stolonifera*, with a subsequent increase of standing crop. Moreover the competitive species *Holcus lanatus* will keep species number low. TURKINGTON et al. (1979) demonstrated that various swards differ greatly in the extent to which they suppress survival of *Trifolium repens* transplants: the sward dominated by *Holcus* > (was more agressive than) *Lolium* > *Agrostis* > *Cynosurus*. A decrease of availability of mineral N or other growth-limiting factors causes a decrease in *Holcus lanatus*, because this species responds both to direct availability of mineral N applied as N fertilizer in a *Holcus/Agrostis* community (Elliott et al. in WATT 1978) and to indirect availability of N resulting from lowering the ground water table in a *Calthion palustris* (GROOTJANS 1979a, b). The number of species may increase at lower standing crop values (GRIME 1979).

Seedling densities generally rise in spring and in summer due to gaps originating spontaneously in winter and summer (GRIME 1979). In this study the spring peak always is found; even with «abandoning» a lot of seedlings emerge. The late summer peaks apparently depend on human interference; hardly any seedlings are found before hay-making, but many seedlings emerge immediately after the cut either in July, or in September. The management practices and the subsequent changes in the vegetation hardly influence the total number of seedlings (*table 3*), whereas the period of peaks in the number of seedlings is

strongly influenced (*fig. 3*). The deviating seedling population, apparently from a persistent seed bank with «July + September hay-making» (*table 1*) could be attributed to the turf being damaged twice a year by heavy machines. We hypothesize that the lack of these species in the other practices implies that the other seedlings predominantly emerge from recently shed seed and/or from a transient seed bank in the turf (THOMPSON & GRIME 1979).

A dense canopy apparently hinders seedlings to become juveniles («abandoning», late spring cohorts, disappearing seedlings of sown species). The positive effect of clipping on seedling survival has been demonstrated by MØLGAARD 1977) and BRANDS & HOEKSTRA (1980); the negative effect of the application of fertilizers causing a dense canopy has been demonstrated by BRANDS & HOEKSTRA (1980). All these finds support the view that the greatest death risk is when the plants are growing in a closing canopy (HARPER 1977). Monocots tend to be positively affected by a short turf after «July hay-making» (*fig. 4*) (1978 is the inexplicable exception with a successful early spring cohort). Dicots may have no ripened seeds at hay-making in July in contrast to the monocots concerned (GROOTJANS 1980). Dicots tend to be positively affected by the short turf created by «September hay-making», both by giving rise to juveniles in autumn and in subsequent spring. After the first cut with «July + September hay-making» a lot of dicots emerge probably from the above hypothesized persistent seed bank by lack of recently ripened seeds, but they do not pass into the juvenile stage, probably due to damaging by the second cut. This view is confirmed by the species sown in November which both with «September hay-making» and with «July + September hay-making» give rise to the largest number of seedlings. Sarukhan & Harper (in HARPER 1977) mention, in contrast to our results, seasonal cycles in seedling mortality, but their results were found with grazing regimes on comparable vegetation structure throughout the year.

From the above we can conclude that apparently a more or less comparable number of safe sites exists for seedling emergence with different management practices. Not all gaps in which seedlings emerge, however, turn out to present safe sites for passing into the juvenile stage, because in that developmental phase management practices determine the fate of seedlings.

The predominant influence of some species upon the structure of the canopy and the resulting decrease and increase of species seem to support the idea that the succession phenomena described can be understood as a consequence of differential growth and different chance of survival of individual species according to the views of DRURY & NISBET (1973) and CONNELL & SLATYER (1977).

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REFERENCES

ARNOLDS, E. J. M. & VAN DER MEIJDEN (1976): *Standaardlijst van de Nederlandse flora 1975.* Mimeographed report. Rijksherbarium, Leiden. 26 pp.

BAKKER, J. P. (1976a): Botanisch onderzoek t.b.v. natuurtechnisch beheer in het Stroomdallandschap Drentsche A. *Natuur en Landschap* **30**: 1–12.

— (1976b): Tussentijdse resultaten van een aantal beheersexperimenten in de madelanden van het Stroomdallandschap Drentsche A. *Contactblad voor Oecologen* **12**: 81–92.

BAKKER, P. A. (1979): Vegetation science and nature conservation. In: *The study of vegetation*, pp. 247–288. Ed. M. J. A. WERGER, Junk, The Hague. 316 pp.

BERGH, J. P. VAN DEN (1979): Changes in the composition of mixed populations of grassland species. In: *The study of vegetation*, pp. 57–80. Ed. M. J. A. WERGER. Junk, The Hague, 316 pp.

BLOM, C. W. P. M. (1977): Effects of trampling and soil compaction on the occurrence of Plantago species in coastal sand dunes. II. Trampling and seedling establishment. *Oecologia Plantarum* **12**: 363–381.

BORG, S. J. TER (1979): Some topics in population biology. In: *The study of vegetation*, pp. 11–56. Ed. M. J. A. WERGER. Junk, The Hague, 316 pp.

BRANDS, H. & E. HOEKSTRA (1980): *De invloed van beheer op vestiging van plantesoorten in graslanden.* Unpublished report.

CAVERS, P. B. & J. L. HARPER (1967): Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. *J. Ecol.* **55**: 59–71.

CONNELL, J. L. & R. O. SLATYER (1977): Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Natur.* **111**: 1119–1144.

COOK, R. E. (1979): Patterns of juvenile mortality and recruitment in plants. In: *Topics in plant population biology.* pp. 207–231. Eds. O. T. SOLBRIG, S. JAIN, G. B. JOHNSON & P. H. RAVEN. Columbia University Press. 589 pp.

DRURY, W. & M. C. NISBET (1973): Succession. *The Arnold Arbor. J.* **54**: 331–368.

GRIME, J. P. (1979): *Plant strategies and vegetation processes.* Wiley, Chichester. 222 pp.

GROOTJANS, A. P. (1979a): Some remarks on the relation between nitrogen mineralization, groundwater table and standing crop in wet meadows (summary). *Acta Bot. Neerl.* **28**: 234–235.

— (1979b): Effecten van grondwaterstandsdaling op een beekdalreservaat in het stroomdallandschap van de Drentse Aa. *W.L.O.-Meded.* **6**: 11–16.

— (1980): The distribution of plant communities along rivulets in relation to hydrology and management. In: *Berichte der Internationalen Symposien der Intern. Ver. für Vegetationskunde* **1979**: 143–170. Cramer Verlag, Vaduz.

GRUBB, P. J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**: 107–145.

HARPER, J. L. (1971): Grazing, fertilizers and pesticides in the management of grassland. In: *The scientific management of animal and plant communities for conservation*, pp. 15–31. Eds. E. DUFFEY & A. S. WATT. Blackwell, Oxford. 652 pp.

— (1977): *Populations biology of plants.* Academic Press, London. 892 pp.

— , J. N. CLARWORTHY, I. H. MCNAUGHTON & G. R. SAGAR (1961): The evolution and ecology of closely realted species living in the same area. *Evolution* **15**: 209–227.

HEUKELS, H. & S. J. VAN OOSTSTROOM (1975): Flora van Nederland. Ed. 18. Wolters-Noordhoff, Groningen.

KLAPP, E. (1965): *Grünlandvegetation und ihre Standort.* Parey, Berlin. 284 pp.

LANGER, R. H. M. (1972): *How grasses grow.* Arnold, Londen. 60 pp.

LAZENBY, A. (1955): Germination and establishment of Juncus effusus. II. The interaction effects of moisture and competition. *J. Ecol.* **43**: 595–605.

LEEUWEN, C. G. VAN (1966): A relation theoretical approach to pattern and process in vegetation. *Wentia* **15**: 25–46.

LEVIN, D. A. & H. W. KERSTER (1974): Gene flow in seed plants. *Evol. Biol.* **7**: 139–220.

LINKOLA, K. (1930): Ueber das Vorkommen von Samenkeimlingen bei Pollakanthen in den natürlichen Pflanzengesellschaften. *Ann. Soc. Zool-Bot. Fennicae Vanamo* **2**: 150–169.

LONDO, G. (1976): The decimal scale for relevés of permanent quadrats. *Vegetatio* **33**: 61–64.

MILES, J. (1973): Early mortality and survival of self-sown seedlings in Glenfeshic. Invernessshire. *J. Ecol.* **61**: 93–98.

— (1974): Effects of experimental interference with stand structure on establishment of seedlings in Callunetum. *J. Ecol.* **62**: 675–687.

— (1979): *Vegetation dynamics.* Chapman, London. 80 pp.

Mølgaard, P. (1977): Competitive effect of grass on establishment and performance of Taraxacum officinale. *Oikos* **29**: 376–382.

NEWBERY, D. McC. (1979): The effects of decomposing roots on the growth of grassland plants. *J. of Appl. Ecol.* **16**: 613–622.

OOMES, M. J. (1976): Vergelijkend beheersonderzoek aan marginale graslanden. *Contactblad voor Oecologen* **12**: 92–99.

— (1977): Cutting regime experiments on extensively used grasslands (summary). *Acta Bot. Neerl.* **26**: 265–266.

RABOTNOV, T. A. (1969): Plant regeneration from seed in meadows of the U.S.S.R. *Herbage Abstr.* **39**: 269–277.

— (1975): On phytocoenotypes. *Phytocoenologia* **2**: 66–72.

RIJKSINSTITUUT VOOR NATUURBEHEER (1979): *Natuurbeheer in Nederland; Levensgemeenschappen.* Pudoc, Wageningen. 392 pp.

SAGAR, G. R. & J. L. HARPER (1960): Factors effecting the germination and early establishment of plantains (Plantago lanceolata, P. media and P. maior). In: *The biology of weeds.* pp. 236–245. Ed. J. L. HARPER. Blackwell, Oxford.

— & A. M. MORTIMER (1976): An approach to the study of the population dynamics of plants with special reference to weeds. *Appl. Biol.* **1**: 1–45.

TAMM, C. O. (1956): Further observations on the survival and flowering of some perennial herbs. I. *Oikos* **7**: 273–292.

THOMPSON, K., J. P. GRIME & G. MASON (1977): Seed germination in response to diurnal fluctuations of temperature. *Nature* **67**: 147–149.

— & — (1979): Seasonal variation in the seed banks of herbaceous species in ten contrasting grassland habitats. *J. Ecol.* **67**: 893–921.

TURKINGTON, R., M. A. CAHN, A. VARDY & J. L. HARPER (1979): The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture. III: The establishment and growth of Trifolium repens in natural and pastured sites. *J. Ecol.* **67**: 231–243.

WATT, T. A. (1978): The biology of Holcus lanatus and its significance in grassland. *Herbage Abstracts* **48**: 195–204.

WESTHOFF, V. (1971): The dynamic structure of plant communities in relation to the objectives of conservation. In: *The scientific management of animal and plant communities for conservation*, pp. 3–14. Eds. E. DUFFEY & A. S. WATT. Blackwell, Oxford. 652 pp.

— &A. J. DEN HELD (1969): *Plantengemeenschappen in Nederland.* Thieme, Zutphen. 324 pp.

— & K. V. SYKORA (1979): A study of the influence of desalinization on the Juncetum gerardii. *Acta Bot. Neerl.* **28**: 505–512.